

Octopus sucker-arm coordination in grasping and manipulation*

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Abstract: In natural settings octopuses use their arms and suckers in a variety of dexterous manipulation tasks, such as extracting prey from crevices and burrows, opening bivalve shells, and arranging middens in front of den entrances. Octopuses use multiple suckers on a single surface for a power grasp that supports their locomotion or permits the animal to carry or move small objects. Similar to squids engaged in prey capture, octopuses can project an arm from their body, attach a group of distal suckers, and pull an object toward themselves by shortening the arm. I investigated octopuses' use of suckers in similar tasks under controlled, reproducible laboratory conditions. Because larger suckers can generate larger adhesion forces, I hypothesized that the larger suckers toward the base of the arm would be preferred in tasks requiring the arm to employ greater forces. Octopuses did not use the strategy found in squid tentacles: applying suckers of appropriate force generation to a surface and lifting or pulling the arm. Instead, in many cases they used a variety of arm movements in combination with different functional groups of suckers. In addition, different arms performed different roles. When animals were restricted to the use of a single arm, they preferred to use suckers in the middle positions of the arm to support this coordinated arm-sucker activity. Contrary to a view of suckers as passive agents reflexively reacting to surface contact, these results are consistent with the known neural organization of the octopus arm and also with complex sucker-arm coordination in the performance of manipulation tasks.

Key words: Octopus, grasping-behavior, suckers, coordination

Octopuses move in a mysterious way. Being flexible, the movements that they make are often difficult to specify and correspondingly difficult to investigate. The literature does not contain a description of octopod walking comparable with descriptions of the six-legged, tripod gait of insects or the stereotyped locomotor patterns of snails or polychaetes. Descriptions of posture run into very similar difficulties and perhaps partly because of this, research on motor control in cephalopods has proved a less attractive proposition than research on sensory analysis and learning. (Wells 1978: 246)

Wells' claim that studies of motor systems in cephalopods have lagged behind those of other sensory and learning systems still rings true today for studies of *Octopus* Cuvier, 1797 and for the reasons he cites. Progress has been made with kinematic descriptions of reaching and fetching behavior that have inspired neural and physiological models of arm control in these activities (Gutfreund *et al.* 1996, 1998, Matzner *et al.* 2000, Sumbre *et al.* 2001, 2005, 2006) and a systematic description of the movements of *Octopus* arms has also been developed (Mather 1998). The muscular-hydrostat mechanisms by which arm movements are effected have provided a conceptual framework for under-

standing limb movement and manipulation in the absence of hard parts (Kier and Smith 1985). In addition, researchers have begun to explore and explain the neurophysiology of bend generation in the arm (Gutfreund *et al.* 1998, Matzner *et al.* 2000, Sumbre *et al.* 2001). However, since Wells (Wells and Wells 1957a, 1957b, Wells 1978), little attention has been directed toward the behavioral repertoire involving the suckers on the arm which provide the octopus with contact tactile and chemosensory information and fine local manipulation.

The arms of octopuses can bring suckers into a position to sense or grasp a surface of interest to the animal. Though the flexibility of their arms makes them quite capable of it, octopuses are rarely observed to wrap their arms to grasp objects. The method octopuses employ in securing purchase on objects varies with the object and context; the wrapping often appears to be a natural continuation of arm momentum following abrupt contact with a fixed object. The suckers are integral to much of the directed behavior of octopuses; Yet, apart from some excellent quantitative studies of their adhesion mechanism (Smith 1991, 1996), their mode of action has received little attention. This report begins to fill this gap by analysis of simultaneous observations of arm movements and the actions of scores of suckers under natural and experimental conditions.

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The extent to which sucker and arm movements are coordinated or independent is currently unknown. Hanlon and Messenger (1996: 15) reflected that “In fact the nervous system of the arms, which contains more neurons than the whole central brain (Young 1971), is in some ways curiously divorced from the rest the brain and many of the arms actions are performed without reference to the brain.” The same comment applies to the relationship of control between the arms and the suckers: suckers have some degree of autonomy but must move in ways that are not in conflict with ongoing arm activity. Studies have shown that a single octopus arm detached from the rest of the animal retains considerable capability for coherent response to stimuli (Wells and Wells 1957a, Rowell 1963, 1966, Altmann 1971, Wells 1978, Gutfreund *et al.* 2006). Yet, all eight arms are not completely independent as is clear because the animal is capable of coordinating all its arms, and arm preferences exist (Byrne *et al.* 2006). These studies have focused on the actions of the arms and not the contributions that the suckers, the primary contact sensing and local action organs, make.

The suckers, too, have the appropriate (direct or indirect) neural connections (Fig. 1A) to send information to and receive information from the brain and the arm on which they are situated (Graziadei 1971). Each sucker has a committed local ganglion. This ganglion receives an enormous number of afferent fibers: chemosensory and mechanosensory axons from the sucker rim as well as proprioceptors (muscle sense) from the various muscles of the sucker. These fibers pass through the nerve connecting the sucker and the ganglion of the sucker (Fig. 1A). This nerve also carries motor neuron axons to control the sucker muscles. The ganglion also carries on bidirectional communication with the main nerve cord of the arm, the chain of brachial ganglia. This communication is carried via the nerve connecting the sucker ganglion to the brachial ganglion (Fig. 1) and not much is known about its function. The brachial

ganglion is one of a chain of ganglia which enlarge, increasing their neuron counts and neuropil volume directly over each sucker. Anatomically, they form a chain of intercommunicating ganglia along the length of the arm, each of which appears to be intimately involved in sucker information processing. Finally, these ganglia make direct connections of their own to the sucker, bypassing the sucker ganglion, through the nerve connecting the brachial ganglion and the sucker (Fig. 1). This nerve carries sensory fibers

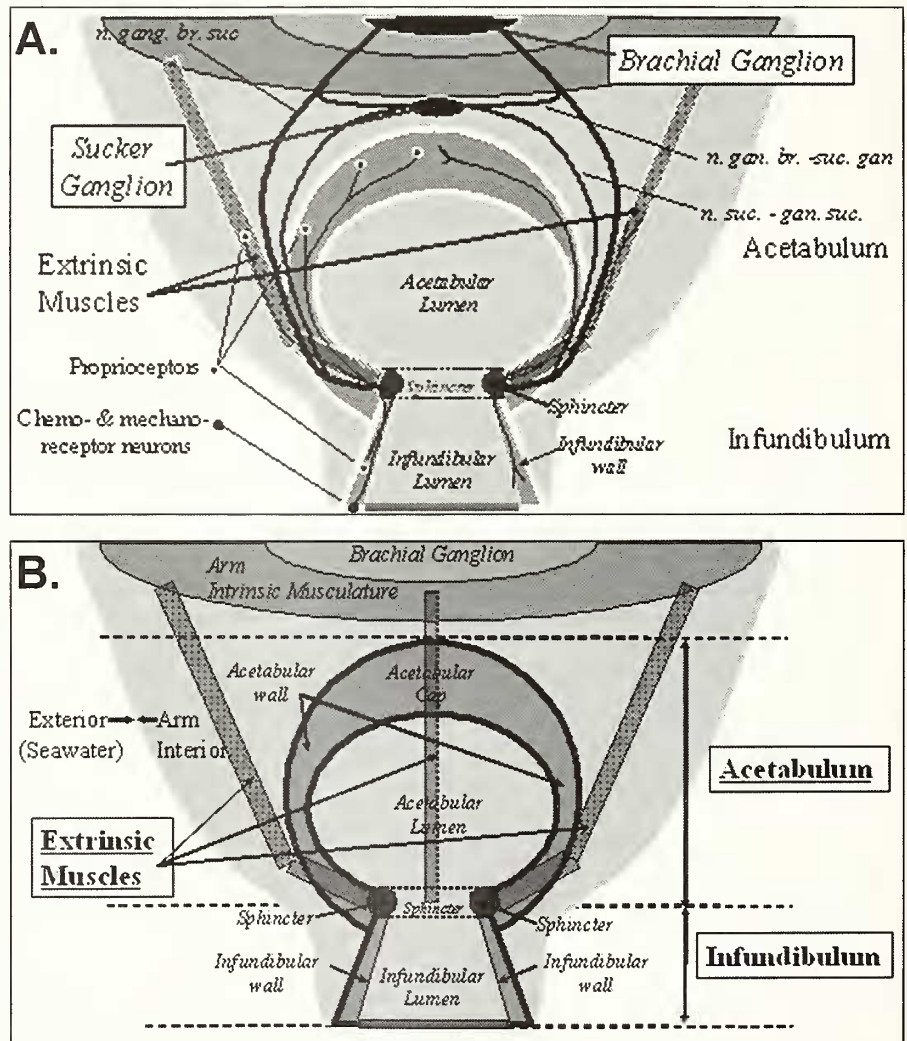


Figure 1. Schematic diagrams of a typical octopus sucker and arm attachment in cross-section perpendicular to the long axis of the arm. A, The functional divisions described in the text for adhesion generation. B, The gross neuroanatomical connectivity of those functional parts in relation to the arm. Abbreviations follow those used in Young (1971): *n.suc.-gan.suc.*, nerve connecting the sucker and the ganglion of the sucker; *n.gang.br.-suc.gan.*, nerve connecting the sucker ganglion to the brachial ganglion; *n.gang.br.-suc.*, nerve connecting the brachial ganglion and the sucker; *n.gan.br.-gan.suc.*, nerve running from the brachial ganglia to the sucker ganglion.

from the sucker and possibly motor fibers to the sucker. This brief sketch of the neuroanatomy demonstrates that the connections exist for rich information exchange between the suckers and the arm chain ganglia and through the brachial ganglia indirectly between the suckers and the brain. The functional roles of these identified pathways have yet to be studied.

In squid tentacles the roles of sucker and tentacle have been studied behaviorally and kinematically and the control of the suckers appears to be much simpler. From these studies it appears that the coordination of limb and sucker action is a passive and not an active one. The squid (*Loligo pealei* Lesueur, 1821) combines the actions of its paired tentacles and suckers in prey capture (Kier 1982, Van Leeuwen and Kier 1997). The terminal club of the tentacle, covered with suckers, is ballistically propelled toward the squid's prey in <300 ms. The process is too fast for tentacle-sucker coordination, so a local reflex-triggered by mechanical contact, in turn triggers rapid sucker attachment. It is possible, despite the anatomical connections described above, that the actions of octopus suckers follows a similar plan where the movements of the arm bring the sucker into contact with some surface, and that surface contact in turn triggers a reflexive sucker attachment. Though there is evidence that this is not always the case (Wells and Wells 1957a, 1957b, Rowell 1963, 1966), the idea that suckers are triggered to attach by mechanical contact is a parsimonious explanation for sucker operation in octopuses that cannot be ruled out in all situations.

Anatomical organization of octopus suckers, which differs in sophistication from those of the squid, indicates that octopus suckers are well suited to support active coordination. The club suckers on the squid tentacle are composed of a single chamber surmounted by a large internal muscle which acts like a piston to develop a negative pressure for adhesion in a few milliseconds (Van Leeuwen and Kier 1997). Octopus suckers are two-chambered, radically-symmetric structures (infundibulum and acetabulum) suspended from the oral surface of the octopus arm that incompletely enclose a volume of the surrounding seawater (Fig. 1B). Like squid suckers, they act on ambient seawater to reversibly attach an object to the octopus arm or the octopus arm to a fixed surface with which the sucker makes contact. The mechanisms by which they facilitate grasping in octopuses have been inferred from anatomy (Kier and Smith 2002). They have an elegant division of function that is absent in the squid: the muscles of the infundibulum reshape the sucker rim to conform to the exterior surface; after a seal is formed (completing the enclosure of the volume), the muscles of the acetabulum expand its internal volume to produce negative pressure (and therefore adhesion force). The major difference between squid tentacle and octopus-arm suckers resides with the third functional group of muscles in the sucker. The

extrinsic muscles of each sucker attach at the junction of the infundibulum and acetabulum and on the arm itself. With the surface held, the extrinsic muscles are arranged to act antagonistically to rotate the sucker rim in virtually any plane around the long axis of the arm, along with whatever it is attached to. It is these extrinsic muscles which suggest octopus suckers evolved to support a *manipulation* as well as *attachment* function.

In addition to this motor function, octopus suckers appear to play an important sensory role. The surface of the octopus arm is studded with mechano- and chemoreceptors but their density is extremely high in the sucker rim: on the order of 10^4 per sucker (Graziadei 1964, Graziadei and Gagne 1976). As mentioned above, these receptors, along with anatomically identified proprioceptors in the sucker, project their axons to make synapses in the small ganglion that lies over each sucker and in the brachial ganglion of the axial nerve cord that runs the length of each arm (Fig. 1B) (Graziadei 1965, 1971). Thus, the observed interconnectivity of the suckers and arm ganglia serve a primarily sensory function rather than a motor control. The receptor and neural organization agree with observations of complex motions made by suckers engaged in apparent sensory exploration. Suckers in an otherwise stationary arm are occasionally observed to reshape themselves by extension, retraction, and rotation to follow surface contours and edges with only the rim in contact and without forming a seal and sucker attachment. These movements occur outside the octopus's field of the vision and therefore appear to require local sensory feedback and motor integration.

The studies reported here sought evidence of active arm-sucker coordination in two forms. First, correlations between arm and sucker activity during spontaneous behavior of freely moving animals were studied. Patterns of activity in groups of suckers that varied with the behavior of the octopus as a whole entity would be consistent with active coordination. Second, I experimentally manipulated the force required to complete a task, thus requiring the octopus employ a different mechanical approach. The adhesive force of suckers is proportional to their size (Smith 1991, 1996) and suckers on any given arm become smaller in size distally (Voight 1993). Thus, if the octopus adjusted the use of its suckers depending upon the force required for a given task, this would provide evidence that some feedback about the appropriate force level was shared between the suckers and the arm or between the suckers and the brain.

MATERIALS AND METHODS

Natural observations of sucker use

Animals

Four wild-caught adult *Octopus bimaculoides* Pickford and McConnaughey, 1949 were filmed in their home tank *ad*

libitum to capture examples of their use of suckers on one vertical glass wall. These animals had arms that were approx. 15-20 cm long at the time of the experiment. I did not determine the sex of these animals. However, one of them showed somewhat enlarged suckers toward the base of its second arms, indicating that this animal was male. The animals were fed *ad libitum* on a diet of clam meat, frozen shrimp, and, occasionally, live crabs. These octopuses were different individuals from those studied in the following experiment.

Video acquisition

Animals were filmed at 30 fps using a JVC MiniDV digital video camera (GR-D250U) positioned outside the tank to encompass the entire pane (resolution ≈ 1 mm per pixel). The tanks were standard 113.59-L tanks of dimensions $76.2 \times 53.34 \times 33.02$ cm. The animals had lived in these tanks for at least 3 weeks and were therefore habituated to the tanks and the conditions in the room where they were housed. Laboratory personnel were absent from the room or visually isolated from the animals by a curtain while the footage was collected. Approx. four hours of this footage was surveyed for periods during which (1) single arms could be observed when (2) 20 or more contiguous suckers were continuously visible for (3) 10-30 seconds. Several sections of video were obtained that I refer to here as "continuous video segments."

Scoring the video

These sections were scored at 1-s intervals. When suckers are attached to a glass surface they assume a characteristic appearance: they are flattened and look like enlarged white discs compared to their unattached state, and the sphincter is clearly visible and round. An observer scored each sucker as "Free" (F), "In-Contact" with the surface (C), "Partially Attached" (P), or "Attached" (A) for each second in each series. Suckers scored as F had no part of the sucker in contact with the glass; C had less than the whole sucker rim in contact with the glass; P had the entire rim but not the sucker sphincter in contact with the glass; and A the entire rim and sphincter were in contact with the glass – the sucker was flat and its radius enlarged. These categories were easy to distinguish. Inter-observer agreement on these categories for a 30-s section of tape in which 45 suckers were visible was at least 95% for three practiced observers.

Analysis

The attachment data were a series of "sucker states" in time. Plots of these data were made to represent the sequence of sucker attachment down the arm. The scored categories of C and P were grouped in a single category while F and A were retained as separate plot categories. I also computed probabilities that a given sucker and its neighbors

would be co-active. For these analyses I assigned each sucker a value of 1 each time it was observed to be in state A and a zero if it were in state F, C, or P. For each time step, I counted the number of coincident attachments for each sucker and its neighbors one, two, three, and more suckers in proximal or distal directions along the arm. With this I had a description of the coincident activation of each sucker with all the observed suckers in a coordinate system centered on the individual sucker. I aligned each individual sucker's co-activation pattern to this sucker-centered frame and, by adding the coincidences for each distance from the sucker, computed the total number of co-incident attachments for each neighbor. This total, divided by the total number of activations observed at that distance, is the proportion of co-activation, or probability of co-activation, observed in that particular frame of a continuous video segment. Individual traces are shown as time series and averages of the entire series (Figs. 2A-C).

Object raising experiments

Experimental animals

The animals used in this experiment were six wild-caught *Octopus bimaculoides*. I did not determine the sex of these animals, but two of them showed somewhat enlarged suckers toward the base of their second arms, indicating that they were male. They had arms 15-20 cm long. This species possesses 150-300 suckers, including extremely small suckers (<1 mm diameter) at the tip, arranged in two staggered rows (Voight 1993). Octopuses were maintained in individual, transparent Plexiglas-walled chambers in a recirculating, artificial seawater system and were fed *ad libitum* on a diet of clam meat, frozen shrimp and, occasionally, live crabs. This did not appear to affect their motivation for capturing live

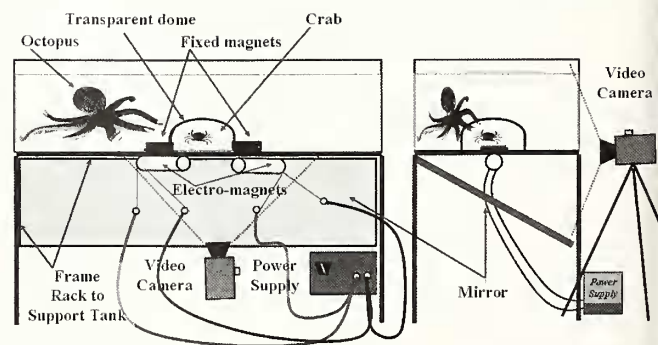


Figure 2. The apparatus used in the dome-raising experiment. The left side of the figure shows a front view of the apparatus and the right, a side-view. The position of the mirror permitted the video capture of a side and bottom view with a single camera. The diagram is schematic and not drawn to scale.

crabs in the testing tank. Animals could see individuals in adjacent chambers but could not make physical contact.

Apparatus

Tests were conducted in a glass-bottomed aquarium (114-L), similar to that used in experiment 1, supplied with continuously refreshed water from the animal's housing system (Fig. 2). A mirror was placed beneath the bottom of the tank at a 45 degree angle so that the octopuses' movements and sucker use could be viewed from below. A single JVC MiniDV digital video camera (GR-D250U) was placed so that half the field of view captured this view from below and half captured the side view of the tank and animal activity. A transparent, ~5-cm diameter glass dome was placed, rim-down, on the floor of the tank. The dome was fitted with two fixed magnets positioned at opposite sides of the rim. These magnets were held to the dome with a single, long cable tie and thermal glue. The magnets were aligned with the positive pole up and the negative down relative to the dome. The fixed magnets' flat surfaces were parallel to the rim of the dome; when the dome was in place, the rim and magnets lay flush with the floor of the tank. Two electromagnets were positioned beneath the tank and aligned with the fixed magnets to provide variable force required to complete the task. Electric current from an Elenco Precision Regulated DC power supply (Model XP-603) was adjusted to modify the strength of the magnetic field they exerted. The force of these activated electromagnets exceeded the force of gravity so that the magnets were held in place. We used a spring scale to determine the force required to detach the dome from the tank floor. We varied the current through the electromagnets over a range of 0 to 1 amperes and recorded the force required to detach the dome at a variety of current levels. A regression analysis of the current supplied to the electromagnets allowed us to estimate the force required to detach the dome ($F = 3.88 C + 10.48$; $r^2 = 0.54$). I could produce a 4 N difference in force due to the action of the magnets. The weak correlation led us to use the settings as "weak" or "strong" magnetic force as conditions in our experiments. The weight of the dome and fixed magnets required 10 N to move when the tank was full of water so the range of forces an octopus was required to apply to detach the dome varied between 10 and 14 N.

Trial procedure

At the start of a trial, a crab (~1-2 cm carapace length) was placed under the dome and the electromagnets were activated to produce the desired level of force. In early trials, the octopus was released into the chamber with the dome and was free to move about the tank and use all of its appendages. On later trials, the animal was released on the other side of a partition with a 1.5 cm hole which permitted

the animal to reach the dome but limited its appendage use to one or at most two arms. The camera recorded the activity of the animal at 30 fps. My protocol called for the termination of the trial if the octopus did not raise the dome within 30 minutes. This time limit was never reached, and the octopuses always raised the dome a few minutes after being placed in the tank.

Scoring the behavior

We scored the number of suckers attached to the dome at the time the dome was raised. The scoring method was the same as that used in the observations reported above (states F, C, P, A). We also scored the portion of the arm in contact with the dome when the animal first raised the dome. The observer judged whether the proximal, middle, or distal third of the arm was in contact with the dome. The time that the dome was first raised was judged as the video frame just before the electromagnets began to fall.

RESULTS

Natural observations of sucker use

Sucker attachments were sparse in the video footage examined. On average $18.07\% \pm 13.78$ (SD) of the suckers observable (20 to 60, depending on the trial) on a given arm were attached at any given time, and instantaneous values ranged from 0 to 39%. We observed no occasions on which all the suckers on an arm were attached—even when the arm was motionless along its entire extent.

The spatial arrangements and temporal sequences of sucker attachment varied with the activity in which the animal and the arm were engaged. Some spatial patterns of simultaneous sucker attachment and certain temporal sequences of attachment were repeated often in these observations.

Adjacent suckers on opposite sides of an arm were frequently observed to attach to the surface in anti-phase: alternating attached and unattached states. Groups of six, ten, or even 15 adjacent suckers would be involved in these coordinated patterns (see Figs. 1B, 2A). Sometimes this would persist as a single alternation; on other occasions it might go on for several seconds, displaying as many as eight cycles of attachment and release. In such an "arm walk", the arm is moved along the surface of the glass, held in a fixed orientation for several seconds as the suckers advanced in leading and trailing pairs across the tank wall.

Suckers could also hold a specific position for periods up to 25 seconds. Interestingly, these patterns of maintained attachment often involved suckers from just one side of the arm (see Figs. 3A-B for examples of this as a horizontal stripe pattern).

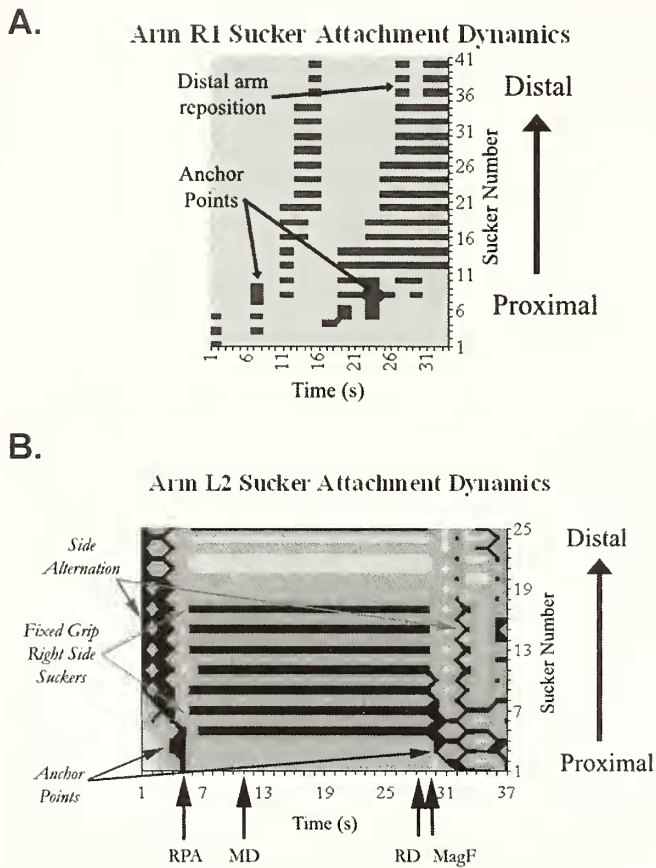


Figure 3. The attachment state of suckers on the arms of two octopuses. The horizontal axis is time measured in seconds. The vertical axis is the sucker number, arranged in sequential order proximally to distally along the arm. The sucker numbers are relative: they are not numbered from the first sucker on the arm. They are simply numbered from the sucker closest the arm base that was visible during the scored observation period. Observations are continuous from that first observable sucker: odd numbered suckers are all on one side of the arm while even numbered suckers are on the other side. Shades of gray represent attachment state. Correlated activity of the arm is marked along the left margin. A, State of 41 suckers on the right first arm (R1) observed over a 37-s period. Dark portions of the plot show attachment, light gray indicates that the sucker was free or in contact with the glass but not sealed. During this period the octopus oriented this arm vertically along the surface of the tank wall as a relatively straight segment. The base of the arm was positioned, and the arm was whipped twice from base to tip in a series of stepped waves. The tip moved freely, its suckers were not scored, and the base was not visible. The horizontal striped pattern results from only suckers on the leading edge of the arm attaching to the surface. Two points marked “anchor points” are groups of attached, adjacent suckers at the start of the move. B, Attachment patterns of 25 adjacent suckers as the animal raised the dome discussed in the text. The grey levels progress from lightest to darkest to indicate “free”, “contact”, “partially attached”,

While both the “arm walk” and continuous attachments described above suggest that suckers that were near neighbors often were not simultaneously attached, we also observed occasions when they were. “Anchor points” (Figs. 3A-B) contrast with the large-scale patterns of coordinated activity described above in that they involved 3-5 adjacent suckers. On these occasions, I observed that the arm was moved by a whip-like motion proceeding from the point of attachment (anchor point) distally. During these arm motions, the distal suckers were unattached and the arm was free to move at all more distal points.

Sometimes the animal would move itself along the tank wall or floor by extending an arm, attaching some of its distal suckers, and then shortening the arm to pull the body toward the attached suckers. When this happened, patterns of coordination involving many and then a few suckers were evident (Fig. 4C). A period of widespread attachments involving 12-15 adjacent suckers on alternating sides of the arm preceded the shortening of the arm. This was followed by a local set of attachments of 2-3 adjacent suckers that supplied the fixed point toward which the animal’s body was moved.

Intermediate-sized adjacent groups of four to eight simultaneously attached suckers were also observed (Fig. 4B). These were observed proximal to a portion of the arm that was extended out from the plane of the tank surface wall.

Object raising experiments

In initial trials, the animals were simply released into the chamber with the dome. The animals were thus free to approach the dome in any manner and free to use all of their arms. The animals invariably draped themselves over the dome, mouth over the dome apex. In the typical posture, the web was expanded over the dome and the arms fell around the sides and made contact with the tank floor. The move-

and “attached” states. The arrows marked RPA, MD, RD, and MagF point to times when the animal **RePositioned** the Arm relative to the dome, the animal **Moved** the **Dome** in a sliding motion along the tank floor, the **Raising** of the **Dome** from the floor of the tank first became visible, and when the **Magnets** holding the dome came **Free** and no longer exerted a force to resist the octopus’s raising. The zigzag patterns visible at the start and end of the plot represent alternate stepping of suckers on opposite sides of the arm. The horizontal striping marks a period of about 20 seconds during which the suckers on just one side of the arm were attached to the dome and during which the octopus was presumably applying a raising force to the dome. Anchor points toward the base of the arm are again visible in this figure. Note, from the absence of light grey, that the majority of the suckers not attached to the dome were in contact with it during this period.

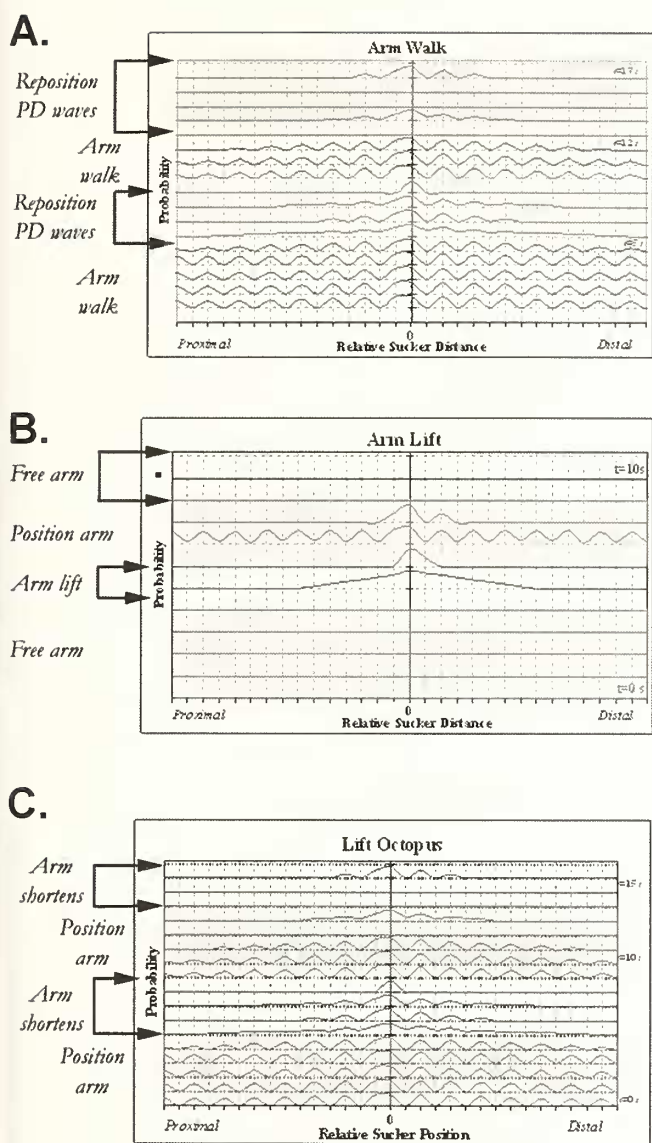


Figure 4. These plots represent the probability of attachment pairs of neighboring suckers during three different types of arm movements. Each line plotted along the vertical axis represents that probability at one second intervals, with earlier traces lower. The horizontal axis represents the distance between neighboring suckers; zero is self (probability always equal to one), negative values are suckers in the proximal direction and positive values are in the distal direction along the arm. Dashed light grey vertical lines mark sucker distance and dashed light grey horizontal lines mark the probability scale (0 to 1) for each trace. A, 41 suckers observed on arm R1 for 20 seconds. During this "arm walk", the octopus moved its arm along the glass with an alternative stepping of the suckers on either side of the arm. This is reflected in the wavy pattern of traces between 0 and 6 seconds and again between 9 and 13 seconds. Between these two periods and after them, the arm was moved by proximal to distal waves along the arm. The widespread patterns of coordinated sucker activity during the walk contrast with local patterns of activity during the wave where anchor points were formed proximally to enable the movement of the arm. B, 10 seconds of observations from 35 suckers on R3. During this period, the octopus moved this arm out away from the surface of the glass using a proximal set of suckers as an anchor for the arm. At 5 seconds, the local neighborhoods spanned 3-5 attached suckers, presumably to support the weight of the arm away from the glass. In the next second, the arm returned to the surface and made several smaller local points of contact. In the following second, a widespread pattern of attachment by suckers on just one side of the arm appeared. This was followed by local groups of suckers in the next second and the movement of the arm from the surface presumably supported by suckers on the other arms. C, Observations of 49 suckers during 16 seconds when the octopus used arm R1 to lift its entire body up the along the tank wall. The octopus projected the arm upward from its body, attached it with distal suckers and then shortened its arm to pull itself upward. The animal repeated this sequence twice during these 16 seconds. In both repetitions there is an initial widespread attachment of suckers on alternative sides of the arms, perhaps probing for a suitable hold, followed by a narrowing to local neighborhoods of attachment during the pulls.

ment and superposition of arms and alteration of suckers made observations of individual suckers and arm usage difficult to assess. However, the general pattern at the moment the dome was raised showed one or more large suckers near the base of the arm(s) attached to the dome, more distal suckers on a variety of arms attached to the floor of the tank with suckers in between unattached to either the floor or the dome. It generally appeared that the lengthening of the arms between the suckers fixed on the dome and those fixed on the tank floor produced the raising of the dome.

Trials with the animal able to reach the dome solely through a hole in a partition permitted unambiguous observation of the actions of the suckers on one arm on the dome and tank floor. In these trials, a pattern of dome-

raising similar in some respects to that in the unrestrained animal was observed. Without exception, the arm extended beyond the partition was draped over the dome. There followed a period of adjustment of arm position and repeated attachment, detachment, and reattachment of individual suckers. At the time of dome raising, there were always suckers attached to the dome as well as suckers attached to the floor of the tank, both proximally and distally from those attached to the dome.

On three single-arm trials, the octopus slid the dome a short distance across the floor of the tank before the dome was raised. These slides were distinct from a pull of the arm toward the animal in that they were made with suckers anchored both proximal and distal to the dome as well as on

the dome itself. They may have been accidentally produced by forces the animal applied to the dome, but on all three occasions the animal released its suckers on the dome and tank floor and repositioned its arm before continuing its efforts to obtain the crab.

All the animals showed a preference for using suckers in the middle of the arm for this task over those at the base or tip. In all six trials with strong and in all six trials with weak magnetic force, the animal used the suckers on the middle of its arm to attach to the dome and the adjacent tank floor (Fig. 5B). A sign test for six trials indicated that these outcomes were unlikely to be due to chance ($S_6 = 6$, $P < 0.05$).

The number of suckers used in strong and weak-magnet trials differed (Fig. 5A). In trials requiring less force, the animals used a mean of 10.16 ± 1.47 suckers while in trials requiring more force they used 15.67 ± 2.58 suckers. While

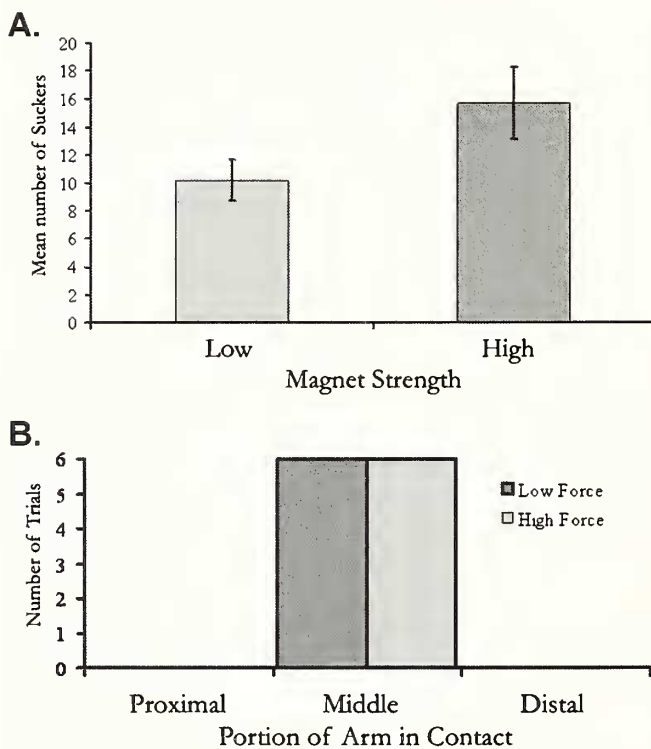


Figure 5. Summary of the results from the dome-raising experiment. A, The average number of suckers used to raise the dome under conditions of high and low force. There is a trend for the number of suckers used to increase with the force required. The means are across animals and the error bars show standard deviation. B, The portion of the arm, divided into rough thirds, used for the raising task during the trial. In all trials all octopuses used the middle portion of their arm regardless of the force required to complete the task.

this difference is in the expected direction, a Student's *t*-test for paired samples did not show that this difference was significant [$t_6 = 1.99$, $P < 0.08$].

DISCUSSION

Here I report both local and distant coordination between suckers. Overall, the results of these studies are consistent with the hypothesis of active arm-sucker coordination and inconsistent with the model of exclusive reflexive sucker control. This conclusion is in agreement with observations made in the course of earlier studies of arm control and tactile discrimination in octopuses (Wells and Wells 1957a, Rowell 1963, 1966, Altmann 1971, Wells 1978, Gutfreund *et al.* 2006).

The patterns of sucker use in freely behaving octopuses varied with the behavior in which the octopus was engaged. Octopus, under conditions in which many suckers were in contact with the surface, attached only a subset of suckers—often a very small subset. A reflex-based mechanism, in which suckers attach when stimulated by an available surface, would show much greater proportions of suckers attached on the types of surfaces used in these studies. This suggests differential control across groups of suckers, at least in the form of inhibition or excitation of attachment at selected suckers, based on information about the overall purpose and state of the ongoing behavior of the animal.

The details of the patterns of sucker use during “arm walk”, “arm lift”, “octopus lift”, and other patterns not described in this report suggest even richer forms of information sharing along the arm to determine which suckers will attach and which will remain free at any given moment. To walk the arm perpendicular to its long axis, the suckers on opposite sides of the arm must be differentially attached and detached in opposing phases. Antagonistic pairs of extrinsic muscles within individual suckers need to pull and push with appropriate timing while the sucker is attached to supply the force necessary to move the arm. This and the other observed patterns of inactivation in adjacent sucker pairs demonstrate a side-to-side level of control of sucker attachment within the arm. “Arm walk” would be facilitated with information about the attachment state of each sucker available to the coordination centers, although a strictly feed-forward system can be imagined. The “arm lift” and “octopus lift” examples break the side-to-side coordination patterns of the “arm walk” by allowing adjacent suckers to attach simultaneously and suggest a different type of sucker control. While the arm-walk patterns are widespread, the sucker attachment patterns in “arm lift” and “octopus lift” are local, presumably concentrating strong attachment forces where they are needed to contribute to the ongoing

behavior. The fact that one of these occurred near the base of the arm and the other near the tip indicates that this control is distributed along the arm and not localized, in this case, to certain portions.

These observations raise the likelihood of many levels of control and coordination of suckers: locally along the arm in neighborhoods of many scales as well as potentially each of those scales in conjunction with the central nervous system.

This absence of localization or, put more succinctly, coordination of distant suckers, is consistent with the known neuroanatomy of the arm. The basic unit (Fig. 1B) is repeated for every sucker down the length of the arm. Above each sucker the associated brachial ganglia is in a position to share information supplied by its sucker with the adjacent ganglia to support such inter-sucker coordination (Graziadei 1971). In a purely reflexive sucker control system, the nerve running from the brachial ganglia to the sucker ganglion (Fig. 1B) would not be required. Only a local circuit from the sucker ganglia to the sucker muscles and from the sucker receptors to the sucker ganglia (Fig. 1B) would suffice. Taken together, our results suggest that the flow of information between the brachial ganglia and their corresponding suckers is not a one-way sensory channel to inform the arm ganglia and possibly the brain about the state of a given sucker. It is instead a two-way channel in which usable information flows from the adjacent suckers to each sucker ganglion and/or sucker. The question of whether or not individual suckers are sometimes activated without influencing other suckers (*i.e.*, through local connections involving a sensory motor arc from the sucker through the sucker ganglion to the sucker muscles without involving brachial ganglionic connections) remains open.

Specialization of sucker operation, to the extent that it exists, is probably physical in nature, following the proximal to distal taper of the arm. Given that larger suckers are capable of supplying greater adhesion forces (Smith 1991) and that larger suckers are found proximally on the arm (Voight 1993), it follows that tasks requiring greater attachment force will likely call for the use of the suckers toward the arm base. Alternatively, they might require the use of more than one sucker since their adhesive force is additive (Smith 1991). In the dome-raising experiment, both of these responses were observed under conditions that varied the required force. The results showed that as the force required to raise the dome increased, so did the number of suckers used. While this result only approached a traditional significance level of 0.05, the trend was in the direction to support our hypothesis. It is worth noting that variability in force generated to hold the dome down was due to the placement of the electromagnets and that the change in required force was only 28% above the force required to raise the dome

alone. It is likely that improvements of this method would reduce experimental error and increase the statistical power of the experimental design. The use of the portion of the middle third of the arm in all trials was contrary to my *a priori* expectations. The larger suckers of the proximal third of the arm were able to reach the dome and I had expected the animal to employ the larger suckers preferentially. The result suggests that, perhaps, the greater flexibility of the middle portion of the arm offered an advantage in completing this task: rather than forming single strong point of attachment on the dome and pulling, the animal produced attachments on the dome and the tank floor on both sides. Thus a trade-off between attachment force and positioning flexibility may occur. The period of probing, contact, and varying attachments/detachments and reattachments that preceded the raising of the dome is consistent with this idea. Information about the force required to raise the dome coming from the suckers could inform arm repositioning. Together these results lead me to tentatively conclude that information about sucker state is available to the arm-control circuits to inform the guidance of arm movements. Given the limitations mentioned above, this conclusion requires confirmation with a more powerful experimental design.

A recent study (Byrne *et al.* 2006) reported that freely moving individuals of *Octopus vulgaris* Cuvier, 1797 that were engaged in visually-guided reaching tasks preferentially make first contact with a target object using the middle of an arm. Byrne *et al.* (2006) were concerned with issues of laterality and arm choice and did not report in detail about the use of suckers in the tasks. Their results implicate visual guidance and, therefore, information from the central nervous system, influencing the part of the arm that is applied to the task and are consistent with the results reported here. It is likely that vision also contributed to octopus performance in the dome raising task. The coincidence of the preference for the middle of the arm in different tasks and in different species is interesting and offers a indication for future studies investigating the relative importance of local and central control mechanisms in the octopus.

In summary, the results of these studies demonstrate that arm-sucker coordination exists almost certainly in the form of descending information influencing sucker activity and very likely in the reverse direction, with sucker state influencing arm movement.

As Wells (1978) wrote over 30 years ago, motor problems in octopuses are rarely studied because of the difficulty of working with such flexible systems. Today we say that these systems are “hyper-redundant”—offering many routes of achieving the same end—but we mean the same thing (Walker *et al.* 2006). An octopus arm with 40 suckers (the

number of contiguous suckers typically observable in these studies) is a subset of the real arm which typically has about 300 suckers (Voight 1993). Even if we limit the actions of the octopus arm to (1) suckers that can only be attached or free and (2) the sections of the arm that link each pair of suckers to 1 pitch, 1 yaw, and 1 roll, we still find that such an arm can be in $\sim 1.2 \times 10^{24}$ states, an enormous number of degrees of freedom. Such an arm has the potential to interact effectively with surfaces far more complex in shape and texture than the smooth glass surfaces used in these studies. Indeed, and the real octopus arm evolved to work on more complex surfaces (*i.e.*, extracting prey from crevices and burrows, opening bivalve shells, and arranging middens in front of den entrances). The studies reported here scratch the surface of an enormous, unexplored domain of complex control methods that we might understand if Wells' challenge of flexibility were pursued. The octopus proves it is possible.

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LITERATURE CITED

- Altmann, J. S. 1971. Control of accept and reject reflexes in the octopus. *Nature* **229**: 204.
- Byrne, R., M. Kuba, D. Meisel, U. Griebel, and J. A. Mather. 2006. Octopus arm choice is strongly influenced by eye use. *Brain Behavior Research* **172**: 195-201.
- Graziadei, P. 1964. Electron microscopy of some primary receptors in the sucker of *Octopus vulgaris*. *Zeitschrift für Zellforschung* **64**: 510-522.
- Graziadei, P. 1965. Muscle receptors in cephalopods. *Proceedings of the Royal Society (B)* **161**: 392-402.
- Graziadei, P. 1971. The nervous system of the arms. In: J. Z. Young, ed., *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford University Press, Oxford. Pp. 45-62.
- Graziadei, P. P. C. and H. T. Gagne. 1976. Sensory innervation of the rim of the octopus sucker. *Journal of Morphology* **150**: 639-680.
- Gutfreund, Y., T. Flash, G. Fiorito, and B. Hochner. 1998. Patterns of arm muscle activation involved in octopus reaching movements. *Journal of Neuroscience* **18**: 5976-5987.
- Gutfreund, Y., H. Matzner, T. Flash, and B. Hochner. 2006. Patterns of motor activity in the isolated nerve cord of the octopus arm. *Biological Bulletin* **211**: 212-222.
- Gutfreund, Y., T. Flash, Y. Yarom, G. Fiorito, I. Segev, and B. Hochner. 1996. Organization of octopus arm movements: A model system for studying the control of flexible arms. *Journal of Neuroscience* **16**: 7297-7307.
- Hanlon, R. T. and J. B. Messenger. 1996. *Cephalopod Behaviour*. Cambridge University Press, Cambridge, UK.
- Kier, W. M. 1982. The functional morphology of the musculature of squid (Loliginidae) arms and tentacles. *Morphology* **172**: 179-192.
- Kier, W. M. and K. K. Smith. 1985. Tongues, tentacles and trunks: The biomechanics of movement in muscular-hydrostats. *Zoological Journal of the Linnean Society* **83**: 307-324.
- Kier, W. M. and A. M. Smith. 2002. The structure and adhesive mechanism of octopus suckers. In: *Symposium on the biomechanics of adhesion*. Anaheim, California.
- Mather, J. A. 1998. How do octopuses use their arms? *Journal of Comparative Psychology* **112**: 306-316.
- Matzner, H., Y. Gutfreund, and B. Hochner. 2000. Neuromuscular system of the flexible arm of the octopus: Physiological characterization. *Journal of Neurophysiology* **83**: 1315-1328.
- Rowell, C. F. H. 1963. Excitatory and inhibitory pathways in the arm of *Octopus*. *Journal of Experimental Biology* **40**: 257-270.
- Rowell, C. F. H. 1966. Activity of interneurons in the arm of *Octopus* in response to tactile stimulation. *Journal of Experimental Biology* **44**: 589-605.
- Smith, A. M. 1991. Negative pressure generated by octopus suckers: A study of the tensile strength of water in nature. *Journal of Experimental Biology* **157**: 257-271.
- Smith, A. M. 1996. Cephalopod sucker design and the physical limits to negative pressure. *Journal of Experimental Biology* **199**: 949-958.
- Sumbre, G., G. Fiorito, T. Flash, and B. Hochner. 2005. Neurobiology: Motor control of flexible octopus arms. *Nature* **433**: 595-596.
- Sumbre, G., G. Fiorito, T. Flash, and B. Hochner. 2006. Octopuses use a human-like strategy to control precise point-to-point arm movements. *Current Biology* **16**: 767-772.
- Sumbre, G., Y. Gutfreund, G. Fiorito, T. Flash, and B. Hochner. 2001. Control of octopus arm extension by a peripheral motor program. *Science* **293**: 1845-1848.
- Van Leeuwen, J. L. and W. M. Kier. 1997. Functional design of tentacles in squid: Linking sarcomere ultrastructure to gross morphological dynamics. *Philosophical Transactions of the Royal Society (Biological Sciences)* **352**: 551-571.

- Voight, J. R. 1993. The arrangement of suckers on octopodid arms as a continuous character. *Malacologia* **35**: 351-359.
- Walker, I. D., D. M. Dawson, T. Flash, F. W. Grasso, R. T. Hanlon, B. Hochner, W. Kier, C. C. Pagano, C. D. Rahn, and Q. M. Zhang 2006. Continuum robot arms inspired by cephalopods. *In: Proceedings of the 2005 SPIE Conference on Unmanned Ground Vehicle Technology IV*. Orlando, Florida.
- Wells, M. J. 1978. *Octopus: Physiology and Behavior of an Advanced Invertebrate*. John Wiley and Sons, New York.
- Wells, M. J. and J. Wells. 1957a. The function of the brain of octopus in tactile discrimination. *Journal of Experimental Biology* **34**: 131-142.
- Wells, M. J. and J. Wells. 1957b. Repeated presentation experiments and the function of the vertical lobe. *Journal of Experimental Biology* **34**: 469-477.
- Young, J. Z. 1971. *The anatomy of the nervous system of Octopus vulgaris*. Clarendon Press, Oxford, UK.

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